

Lack of evidence that Tonkean macaques understand what others can hear

Morgane Costes-Thiré · Marine Levé ·
Pierre Uhlrich · Arianna De Marco ·
Bernard Thierry

Received: 20 June 2014 / Accepted: 30 July 2014 / Published online: 14 August 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract By distinguishing the attentional cues of their mates, animals can learn what part of their environment is of potential interest. However, recognizing the attentional states of others through auditory perception appears to be difficult, since these states are generally not accompanied by ostensive signals liable to reveal them. In this context, one study found that rhesus macaques withhold their action when unobserved, then concluding that they know what others can hear. We replicated this study by testing 18 Tonkean macaques in an experimental setting where subjects had to choose between two boxes containing a food reward. One box made a noise when opened, and the other opened silently. An experimenter was present and could either have her back to subjects or be facing them. If subjects aimed to avoid attracting the experimenter's attention, they were expected to select the silent box while the experimenter's back was turned. Results showed that subjects did not discriminate between boxes, whatever the

experimenter's position. We thus found no evidence that Tonkean macaques are able to take the auditory attentional states of a human into account. It is therefore premature to conclude that monkeys can establish a link between hearing and knowing.

Keywords Social cognition · Attentional state · Audition · Deception · Primates · *Macaca tonkeana*

Introduction

By recognizing the attentional cues of partners, animals can learn what part of their environment is of potential interest. By detecting when rivals direct their attention toward them, they may also implement tactics to deceive the audience. Deception has been reported in various species of corvids and non-human primates (Emery and Clayton 2009; Byrne 2010), and its most common form is the withholding of information: An individual avoids indicating the location of a resource by refraining from looking, approaching or retrieving it, for example (Menzel 1974; Coussi-Korbel 1994; Ducoing and Thierry 2003). In order to mislead conspecifics—and leaving aside the question of theory of mind, i.e., whether bystanders read behaviors or mental states—the withholder has to inhibit certain behaviors on noticing that it is being monitored.

Most experiments regarding the understanding of attentional states have dealt with visual perception. Animals like domestic dogs and non-human primates can use human face or body orientation as an indication of monitoring (Call et al. 2003; Kaminski et al. 2004; Bulloch et al. 2008; Hattori et al. 2010; Tempelmann et al. 2011; Maille et al. 2012), and many mammals and birds are sensitive to gaze or even able to follow a gaze, i.e., look where someone else is looking (Tomasello et al. 1998; Emery and Clayton 2009; Davidson et al. 2014).

M. Costes-Thiré · M. Levé · P. Uhlrich · B. Thierry (✉)
Département Ecologie, Physiologie et Ethologie,
Centre National de la Recherche Scientifique,
Strasbourg, France
e-mail: bernard.thierry@iphc.cnrs.fr

M. Costes-Thiré · M. Levé · P. Uhlrich · B. Thierry
Institut Pluridisciplinaire Hubert Curien, Université de
Strasbourg, Strasbourg, France

A. De Marco
Fondazione Ethoikos, Radicondoli, Italy

A. De Marco
Parco Faunistico di Piano dell'Abatino, Poggio San Lorenzo,
Italy

A. De Marco
Istituto di Scienze e Tecnologie della Cognizione, Consiglio
Nazionale delle Ricerche, Rome, Italy

Several studies have produced negative results, showing that animals have difficulties identifying visual attention direction, and pointing out that congruent postural cues and/or short stimulus distance favor success (Povinelli and Eddy 1996a, b; Itakura et al. 1999; Vick and Anderson 2000; Schloegl et al. 2007; Bulloch et al. 2008; Téglás et al. 2012). Remarkably, domestic dogs (Call et al. 2003; Gácsi et al. 2004), monkeys (Flombaum and Santos 2005; Hattori et al. 2010; Bourjade et al. 2014) and great apes (Hostetter et al. 2007; Bania and Stromberg 2013) can distinguish between closed and open eyes, raising the question of whether they understand visual attention or whether they become sensitive to gaze through associative learning.

Recognizing the attentional states of others appears to be especially tricky in the case of auditory perception since these events are generally not accompanied by ostensive signals similar to the head and eyes moves associated to visual perception. Even in non-social situations, reasoning in the auditory domain is cognitively more demanding than in the visual domain, as shown in experiments where individuals have to use either the presence or the absence of a reward in one container to infer its absence or presence in a second container. In all monkeys and great apes tested, a recurrent finding is that this task is easier to solve in its visual modality when subjects have to deal with visible or invisible food rewards than in its auditory modality when they have to take into account either the sound produced by a baited container being shaken or the absence of noise associated with an empty container (Call 2004; Sabbatini and Visalberghi 2008; Paukner et al. 2009; Schmitt and Fischer 2009; Heimbauer et al. 2012; Petit et al. 2005).

To test the ability of monkeys to recognize auditory perception, Santos et al. (2006) have studied rhesus macaques (*Macaca mulatta*) in a situation where the subject had to approach an experimenter and choose between two baited boxes, one of which made a noise if opened and the other opening silently. When the experimenter looked at the subjects, none of them displayed a significant preference for any particular box. When the experimenter did not look at the subjects, they tended to select the silent box. The investigators concluded that monkeys chose the silent box in order to withhold their action from the experimenter's attention, and claimed that rhesus macaques understand the connection between hearing and knowing, implying that they can attribute intentions to others (Santos et al. 2006). In a similar study carried out by Melis and collaborators (2006), chimpanzees (*Pan troglodytes*) had to steal food from an experimenter by choosing between two baited boxes, one silent and the other making noise when opened, and it appeared that chimpanzees too preferentially selected the silent box when unobserved. Both teams concluded that subjects understand the connection between hearing and knowing, which implies that they can attribute intentions to others. Such a conclusion is in line with

what we know about chimpanzees since converging evidence indicates that they have some understanding about the mental states of others (Hare et al. 2001; Call and Tomasello 2008). By contrast, monkeys generally fail in tasks requiring them to attribute mental states (Suddendorf and Whiten 2001; Hare et al. 2003; Cheney and Seyfarth 2007), thus it may be asked how they could infer perceptual states. It should be added that in a further experiment between competing chimpanzees, subjects did not take into account whether a dominant partner had heard a container being noisily baited compared to another that they could not hear being baited (Bräuer et al. 2008). Contrary to the previous two experiments, however, there was a delay between hearing the noise and the food competition, and the competitor was out of view when it was supposed to be listening, which may have been more demanding in terms of cognitive inference (Emery and Clayton 2009).

These inconsistencies prompted us to replicate the study of Santos and collaborators in Tonkean macaques (*Macaca tonkeana*). In cognitive tasks, this species has been shown capable of tool use (Anderson 1985; Ducoing and Thierry 2005), inference by exclusion (Petit et al. 2005) and long gratification delays (Pelé et al. 2011). In food-searching tasks, subordinate Tonkean macaques have already been observed using information-withholding tactics in the presence of dominant freeloaders. They avoided approaching the food, or walked away from it (Ducoing and Thierry 2003, 2004). We tested Tonkean macaques in an experimental situation similar to those devised by Santos et al. (2006). Subjects had to approach an experimenter who was either watching them or not, and choose between two baited boxes fitted with pellet bells. The bells jingled on one box when it was opened, whereas the other remained silent because the ringers had been removed from the bells. Contrary to the study by Santos and collaborators, in which subjects had been tested without previous training, we habituated the subjects to the apparatus prior to testing, thus giving them an opportunity to learn that boxes could produce a sound or not when opened. We made the following predictions: (1) If subjects aimed to avoid attracting the experimenter's attention, they should select the silent box when the experimenter's back is turned, but they should not discriminate between boxes when the experimenter deters deception by looking toward them; (2) If subjects did not account for the experimenter's auditory perception, they should not discriminate between the boxes in either condition.

Methods

Subjects

We studied 21 Tonkean macaques maintained at the Parco Faunistico di Piano dell'Abatino Rescue Centre in Rieti,

Italy. Their age and sex are presented in Table 1. All were born in captivity and belonged to four different social groups (group C, 11 individuals; D, 15; E, 13; F, 5) originating from the same population (Thierry et al. 1994; De

Marco et al. 2011). Each group was housed in an enclosure approximately 500 m² and 5 m high, furnished with wooden structures, perches and ropes, and including a shelter. Animals were never deprived of food. They were fed with commercial diet pellets, fresh fruit and vegetables. Water was available ad libitum. For testing, positive reinforcement was used to temporarily separate subjects from the rest of the group and place them in an individual compartment. The subjects selected for testing were all individuals that accepted to enter the compartment and take part in the experiment.

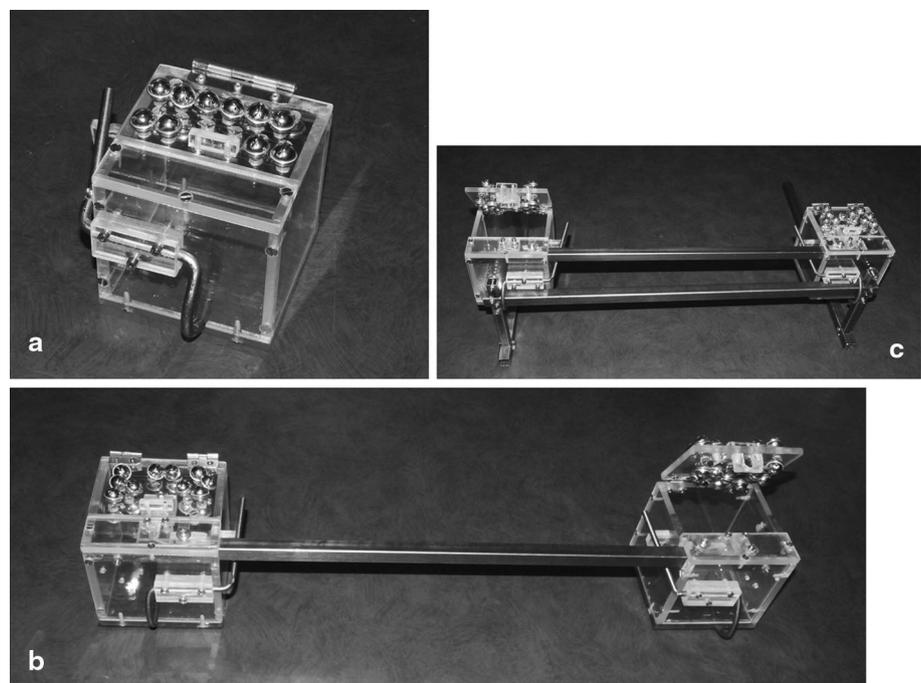
Table 1 Age, sex and groups of subjects

Name	Age in years	Sex	Group
Nat	13	Male	F
Nab	13	Male	C
Rim	11	Male	E
Cha	11	Male	D
Sib	10	Female	E
Dan	10	Female	D
Don	10	Male	D
Sho	10	Male	E
Tet	9	Female	E
Tan	8	Female	E
Fle	8	Female	D
Utt	8	Male	E
Gra	6	Male	D
Nim	6	Male	F
Gua	5	Female	D
Dat	5	Male	D
Cou	5	Male	D
Soq	5	Male	C
Gue	3	Female	D
Arj	3	Male	E
Ann	3	Male	E

Apparatus

The boxes measured 10 × 10 × 10 cm and were made of clear plastic. A hinged lid could be opened to access their content. Both sides of each box lid were covered with 15-mm-diameter gilded brass pellet bells (ten bells on each side, Fig. 1a). “Noisy boxes” were fitted with intact bells that rang when the lid was lifted. “Silent boxes” had bells with their ringers removed, so they could be opened without producing any sound. Both kinds of boxes were visually identical. To avoid further noise, lids were constructed so as to not close under their own weight. Separate boxes were used in the first period of training, but were replaced in the following periods by an experimental apparatus made of two boxes, one noisy and the other silent, linked by a hollow steel bar 45 cm long (Fig. 1b). The bar contained a system of strings and pistons operating in such a way that opening one box mechanically locked

Fig. 1 Experimental apparatus. **a** Box fitted with pellet bells and a hooked tab. **b** Two-box apparatus. **c** Apparatus hitched to support structure



the other, so only one box could be opened at a time. We constructed two of these two-box systems, one with the noisy box on the left and the silent one on the right, and a second with these positions inverted. During the experiments, we hitched the apparatus to a metal support structure to ensure stillness (Fig. 1c) and placed it 5 cm from the fence of the compartment housing the subject. The latter could open boxes by putting its hand through the fence.

Training phase

To habituate monkeys to pellet bells, we hung two rings of bells, one noisy and the other silent, to the fence of each group's enclosure for 3 weeks. During the same period, we conducted a 1-h daily session in which we proposed to all members of each group two separate boxes in front of the fence, one noisy and the other silent, which they had to learn to open in order to reach the pieces of apple they contained.

The subjects learned to get rewards from the two-box apparatus during a second period. An experimenter (M. Costes-Thiré) helped by an assistant (M. Levé) used the apparatus to carry out in two training sessions of 12 trials each for each individual. In the first session, a cookie food reward was placed in one of the boxes of the apparatus in a randomized order, 6 times on the left and 6 times on the right. Half of the subjects were presented with the apparatus with noisy bells on the left in the first 6 trials and the apparatus with noisy bells on the right in the last 6 trials. We inverted both conditions for the other subjects. In each trial, the experimenter's assistant sat 3 m away from the fence, level with the subject to avoid any eye contact between them. The assistant reported the subject's actions to the experimenter, timed the trials and recorded their outcomes. The experimenter first placed a cookie in one box out of the subject's sight, then she approached the fence and showed the monkey that one box was filled and the other empty. She hitched the apparatus to the support structure before taking position 3 m away with her back to the subject. The latter had to open the box to take the reward. The experimenter removed the apparatus 10 s after the subject had taken the reward, unless it attempted to open the second box, in which case a further 10 s were counted before unhitching the apparatus. The experimenter waited 30 s after the end of food consumption before beginning another trial. Only subjects who succeeded in 11 out of 12 trials took part in the second training session. If they did not manage, we ran the first session with them again. Seventeen of the twenty-one subjects were successful in one session, three succeeded in two sessions, and one succeeded in three sessions.

The conditions of the second training session were identical to those of the first, except that both boxes

contained a cookie. This session was designed to show subjects that they could gain a single cookie, the second box being locked thereafter. In each trial, the experimenter approached the fence and showed the subject that one box was noisy and the other silent by opening and closing the lid of each box successively. She then hitched the apparatus to the support structure. To ensure that subjects did not have a tendency to select the same side, we required subjects to open each of the two boxes at least twice during the session before continuing to the testing phase. If the two boxes were not opened, subjects were submitted to the whole training procedure once again, i.e., the first and second sessions. Eighteen individuals succeeded in a single session, and three had to renew both sessions once to reach the criterion.

Testing phase

Each subject took part in a two-trial session using two baited boxes. Three conditions were liable to affect the choices made by the monkeys: (1) the asymmetry of the two-box apparatus with noisy and silent bells on each side; (2) the side first shown by the experimenter; (3) the side first hitched to the support by the experimenter. We therefore counterbalanced these three left/right conditions between subjects, attributing each individual with a randomly chosen combination of conditions for each session. Video recording of the session focused on the apparatus and the subject.

To incite monkeys to avoid alerting the experimenter's attention by making noise, we made her unrecognizable and even intimidating by dressing her in a green jumpsuit, gloves, overshoes and a hood allowing only the eyes to be seen. At the beginning of a trial, the experimenter approached the enclosure without looking at the subject. She stopped 3 m away from the fence and looked at the ground. Out of the subject's sight, the assistant placed a cookie in each box then approached the fence, caught the subject's attention and demonstrated the opening and closing of each box before going to sit at her usual location. The experimenter then approached the fence and hitched the apparatus to the support structure. The experimenter's behavior and position differed in the two trials: In trial 1, she approached without looking at the subject before withdrawing to sit 3 m away with her back to the monkey, whereas in trial 2 she looked toward the subject before returning to sit facing the subject, looking in its direction with her gaze focused on the middle of the apparatus bar.

In order to validate a trial, the subject had to retreat at the experimenter's approach. If this did not occur, the trial was interrupted and repeated the next day with the experimenter wearing a white jumpsuit that was usually worn by care staff to capture the animals. A refusal to approach the apparatus was also possible: If a subject did not open a box

after 2 min, the trial was interrupted and scheduled for the next day; this time the experimenter was dressed in normal clothes but wore a mask covering the lower face. Fifteen subjects were tested in sessions with the green jumpsuit, four with the white jumpsuit, and two with the mask. Two individuals (Don, Arj) did not retreat at the approach of the experimenter dressed in white, and another (Tet) never came to open a box even when the experimenter wore a mask, so they were excluded from the study.

Data analysis

Video footage was processed by a collaborator (P. Uhrich) who was uninformed about the experimental conditions. He recorded which box was opened by subjects and measured their response latency, i.e., the time interval between the hitching of the apparatus and the box being opened.

We used the binomial test to compare the number of noisy and silent box choices in each trial, and the Fisher exact test to compare the performances of subjects in both trials. We also compared response latencies in both trials using the Wilcoxon matched-pairs test. Statistical tests were computed using the R software (version 3.0.1.). The significance level was set at 0.05.

Results

The comparison of the response latencies of subjects did not reveal statistically significant differences between trials 1 and 2 (experimenter with back turned to subject: mean \pm SD = 49.2 \pm 40.4 s; experimenter facing subject: mean \pm SD = 29.1 \pm 31.8 s; Wilcoxon test, $N = 18$, $V = 45$, $P = 0.142$). When the experimenter had her back to the subject (trial 1), an equal number of individuals chose one box or the other (noisy: $N = 9$; silent: $N = 9$; binomial test, $P = 1$). When the experimenter was facing the subject (trial 2), 6 individuals selected the noisy box and 12 the silent one (binomial test, $P = 0.333$). Therefore, we did not find any significant preference for the noisy or the silent box in monkeys, whatever the experimental conditions. Correspondingly, a comparison of the choices made by subjects in both trials did not yield a statistically significant difference (Fisher exact test, $P = 0.500$) (Fig. 2).

Discussion

We placed Tonkean macaques in a situation where they could avoid making noise while taking food in the presence of an experimenter who could not see them. We did not find any evidence that they took the experimenter's hearing into account, since they did not appear to discriminate between

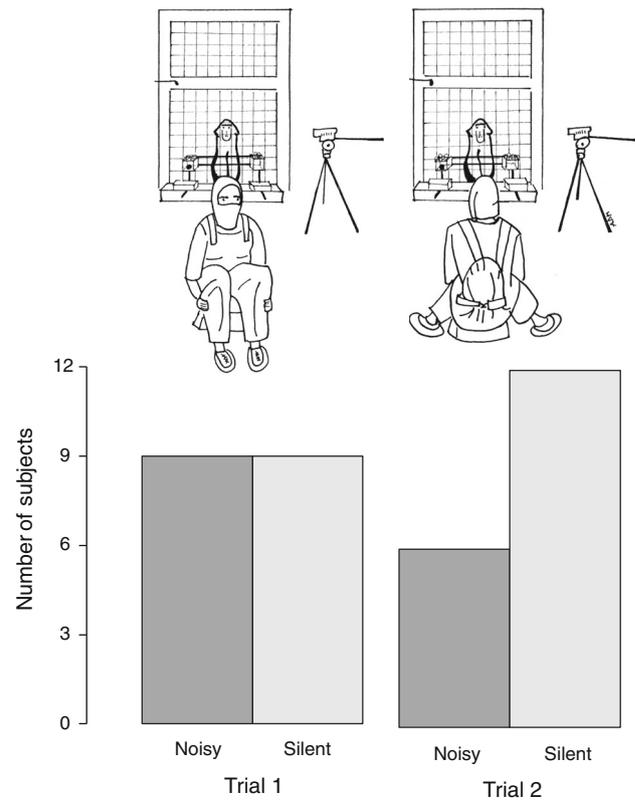


Fig. 2 Number of subjects that opened noisy and silent boxes during trial 1 (experimenter turning back to subject) and trial 2 (experimenter facing subject)

silent and noisy baited containers, whether the experimenter was facing them or had her back to them. These results contrast with those of Santos et al. (2006) whose report that rhesus macaques targeted the silent container more often when the experimenter was not looking at them suggested that monkeys could deceive a human based on the understanding of auditory perceptual states.

Several factors could be called upon to explain such a discrepancy. First of all, Santos and collaborators tested rhesus macaques, whereas we tested Tonkean macaques, and it may be asked whether the former could be better at reasoning than the latter. However, no major difference has been reported so far in the cognitive performances of macaque species. Tonkean macaques not only appear to be more responsive than rhesus macaques in object exploration tasks (Thierry et al. 1994) but also perform better in experiments requiring individuals to use visual or auditory cues to locate food rewards (Petit et al. 2005). There is thus no reason to consider a contrario that rhesus macaques would be more skillful in processing information than Tonkean macaques.

Secondly, there were several differences in experimental procedures between the two studies. The apparatus used by Santos and collaborators was limited to two independent boxes fitted with either noisy or silent pellet bells. Our will

to make subjects repeatedly experience the sounding dimension of the test before the sessions began required the designing of a more complex, two-box apparatus that could be baited with two rewards but would only provide one. Prior to testing, Tonkean macaques first had the opportunity to accustom themselves to the jingling produced by bells or the absence of jingling. Thereafter, training sessions allowed them to familiarize themselves with the experimental procedure and the sound asymmetry of the two-box apparatus. This contrasts with the inexperience of the subjects taking part in Santos and collaborators' trials; rhesus macaques were not familiar with the experimental procedure and had probably never seen or heard a pellet bell prior to the trial, making the fact that they could immediately adopt a tactic aiming to deceive human auditory attention all the more surprising. In any case, the negative results in Tonkean macaques can hardly be explained by a lesser acquaintance with experimental conditions compared to rhesus macaques.

Thirdly, it may be asked whether Tonkean macaques were as motivated as rhesus macaques to avoid alerting the experimenter. The semi-free ranging monkeys studied by Santos and collaborators had to approach an experimenter sitting approximately 2 m away, with no fence separating them. We learned from our preliminary observations that most Tonkean macaques were not willing to approach an experimenter dressed in green and wearing a mask sat <2 m from the fence, even when she had her back to them, so we fixed the distance at 3 m. In our experiments, subjects retreated at the approach of the experimenter at first, and their response latencies before opening a box averaged 30 s or more, which compares well with the behavior of rhesus macaques: Although the latter's response latencies were not quantified in the study by Santos and collaborators, they were allowed 1 min to approach and touch a box. Therefore, it can be fairly estimated that the presence of unknown humans intimidated monkeys to a similar extent in both studies. It should be added that Santos and collaborators described their experimental situation as based on food competition between subjects and human beings, but experimenters actually proposed food to subjects and no attempt was made to simulate any food stealing, so that subject intimidation as induced by the presence of unknown experimenters may have prevailed. This contrasted with the study of Melis and collaborators (2006) in which chimpanzees participated prior to testing in warm-up motivation trials where they had to compete for food with the experimenter.

We know that Tonkean are able to conceal information (Ducoing and Thierry 2003, 2004). In the event that they do not take human hearing into account, this does not necessarily mean that individuals cannot suppress sound when circumstances demand it. It is common observation that many predators become silent at the approach of their prey, and laboratory experiments have demonstrated that species

like food-storing corvids and domestic dogs can avoid making noise in competitive situations (Stulp et al. 2009; Shaw and Clayton 2013; Bräuer et al. 2013; Kaminski et al. 2013). However, animals may learn to associate the need for silence and the presence of others to achieve their goals without necessarily understanding perceptual states. Claiming that subjects are aware of auditory perceptual states implies that not only they recognize the affordance of sounds with regard to the behavior of bystanders but also they understand the perspective of other individuals (Santos et al. 2006; Emery and Clayton 2009; Shaw and Clayton 2013). At present, only great apes like chimpanzees are known to reliably attribute knowledge and ignorance in others (Call and Tomasello 2008), whereas monkeys do not (Suddendorf and Whiten 2001; Hare et al. 2003; Burkart and Heschl 2007; Cheney and Seyfarth 2007; but see Marticoarena et al. 2011; Overduin-de Vries et al. 2014).

It should be added that we cannot exclude the possibility that contingency learning may lead animals to specifically suppress noise when they are looked at. This achievement seems unlikely in many animals, given that the circumstances needed for such learning to occur are rarely available. These conditions may be present in dogs, however, owing to their common life with humans. This would explain that dogs preferentially consumed food from a silent container when observed by a human gatekeeper, whereas they did not distinguish between silent and noisy containers when unobserved (Kundey et al. 2010). In contrast to other studies, however, dogs were told not to take the food. It is possible that they had already had many opportunities to learn that they can disobey whenever their owner is looking elsewhere, provided they act silently.

To conclude, Tonkean macaques failed to take the auditory attentional states of a human into account in our experimental conditions, which is at odds with the performances reported in rhesus macaques (Santos et al. 2006). We consider that it is premature to assert that monkeys can establish a link between hearing and knowing. Clearly, more research in a larger sample of individuals and species will be necessary to settle this important issue.

Acknowledgments We are grateful to the staff of the *Parco Faunistico di Piano dell'Abatino* of Rieti for their unremitting support, and to O. Petit and V. Dufour for their fruitful comments.

References

- Anderson JR (1985) Development of tool-use to obtain food in a captive group of *Macaca tonkeana*. *J Hum Evol* 14:637–645
- Bania AE, Stromberg EE (2013) The effect of body orientation on judgments of human visual attention in western lowland gorillas (*Gorilla gorilla gorilla*). *J Comp Psychol* 127:82–90

- Bourjade M, Meguerditchian A, Maille A, Gaunet F, Vauclair J (2014) Olive baboons, *Papio anubis*, adjust their visual and auditory intentional gestures to the visual attention of others. *Anim Behav* 87:121–128
- Bräuer J, Call J, Tomasello M (2008) Chimpanzees do not take into account what others can hear in a competitive situation. *Anim Cogn* 11:175–178
- Bräuer J, Keckeisen M, Pitsch A, Kaminski J, Call J, Tomasello M (2013) Domestic dogs conceal auditory but not visual information from others. *Anim Cogn* 16:351–359
- Bulloch MJ, Boysen ST, Furlong EE (2008) Visual attention and its relation to knowledge states in chimpanzees, *Pan troglodytes*. *Anim Behav* 76:1147–1155
- Burkart JM, Heschl A (2007) Understanding visual access in common marmosets, *Callithrix jacchus*: perspective taking or behaviour reading? *Anim Behav* 73:457–469
- Byrne RW (2010) Deception: competition by misleading behavior. In: Breed MD, Moore J (eds) *Encyclopedia of animal behavior*, vol 1. Academic Press, Oxford, pp 461–465
- Call J (2004) Inferences about the location of food in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *J Comp Psychol* 118:233–241
- Call J, Tomasello M (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn Sci* 12:187–192
- Call J, Bräuer J, Kaminski J, Tomasello M (2003) Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *J Comp Psychol* 117:257–263
- Cheney DL, Seyfarth RM (2007) *Baboon metaphysics*. University of Chicago Press, Chicago
- Coussi-Korbel S (1994) Learning to outwit a competitor in mangabeys (*Cercocebus torquatus torquatus*). *J Comp Psychol* 108:164–171
- Davidson GL, Butler S, Fernández-Juricic E, Thornton A, Clayton NS (2014) Gaze sensitivity: function and mechanisms from sensory and cognitive perspectives. *Anim Behav* 87:2–15
- De Marco A, Cozzolino R, Dessì-Fulgheri F, Thierry B (2011) Collective arousal when reuniting after temporary separation in Tonkean macaques. *Am J Phys Anthropol* 146:457–464
- Ducoing AM, Thierry B (2003) Withholding information in semifree-ranging Tonkean macaques (*Macaca tonkeana*). *J Comp Psychol* 117:67–75
- Ducoing AM, Thierry B (2004) Following and joining the informed individual in semifree-ranging Tonkean macaques (*Macaca tonkeana*). *J Comp Psychol* 118:413–420
- Ducoing AM, Thierry B (2005) Tool-use learning in Tonkean macaques (*Macaca tonkeana*). *Anim Cogn* 8:103–113
- Emery NJ, Clayton NS (2009) Comparative social cognition. *Annu Rev Psychol* 60:87–113
- Flombaum JJ, Santos LR (2005) Rhesus monkeys attribute perceptions to others. *Curr Biol* 15:447–452
- Gácsi M, Miklósi A, Varga O, Topál J, Csányi V (2004) Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Anim Cogn* 7:144–153
- Hare B, Call J, Tomasello M (2001) Do chimpanzees know what conspecifics know? *Anim Behav* 61:139–151
- Hare B, Addessi E, Call J, Tomasello M, Visalberghi E (2003) Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Anim Behav* 65:131–142
- Hattori Y, Kano F, Tomonaga M (2010) Differential sensitivity to conspecific and allospecific cues in chimpanzees and humans: a comparative eye-tracking study. *Biol Lett* 6:610–613
- Heimbauer LA, Antworth RL, Owren MJ (2012) Capuchin monkeys (*Cebus apella*) use positive, but not negative, auditory cues to infer food location. *Anim Cogn* 15:45–55
- Hostetter AB, Russell JL, Freeman H, Hopkins WD (2007) Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. *Anim Cogn* 10:55–62
- Itakura S, Agnetta B, Hare B, Tomasello M (1999) Chimpanzee use of human and conspecific social cues to locate hidden food. *Dev Sci* 2:448–456
- Kaminski J, Call J, Tomasello M (2004) Body orientation and face orientation: two factors controlling apes' begging behavior from humans. *Anim Cogn* 7:216–223
- Kaminski J, Pitsch A, Tomasello M (2013) Dogs steal in the dark. *Anim Cogn* 16:385–394
- Kundey SMA, De Los Reyes A, Taglang C, Allen R, Molina S, Royer E, German R (2010) Domesticated dogs (*Canis familiaris*) react to what others can and cannot hear. *Appl Anim Behav Sci* 126:45–50
- Maille A, Engelhart L, Bourjade M, Blois-Heulin C (2012) To beg, or not to beg? That is the question: mangabeys modify their production of requesting gestures in response to human's attentional states. *Public Libr Sci One* 7:e41197
- Martcorena DCW, Ruiz AM, Mukerji C, Goddu A, Santos LR (2011) Monkeys represent others' knowledge but not their beliefs. *Proc R Soc B* 14:1406–1416
- Melis AP, Call J, Tomasello M (2006) Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *J Comp Psychol* 120:154–162
- Menzel EW (1974) A group of young chimpanzees in a one-acre field. In: Schrier AM, Stollnitz F (eds) *Behavior of non-human primates*. Academic Press, New York, pp 83–153
- Overduin-de Vries AM, Spruijt BM, Sterck EHM (2014) Long-tailed macaques (*Macaca fascicularis*) understand what conspecifics can see in a competitive situation. *Anim Cogn* 17:77–84
- Paukner A, Huntsberry ME, Suomi SJ (2009) Tufted capuchin monkeys (*Cebus apella*) spontaneously use visual but not acoustic information to find hidden food items. *J Comp Psychol* 123:26–33
- Pelé M, Micheletta J, Uhrlich P, Thierry B, Dufour V (2011) Delay maintenance in Tonkean macaques (*Macaca tonkeana*) and brown capuchin monkeys (*Cebus apella*). *Int J Primatol* 32:149–166
- Petit O, Call J, Thierry B (2005) Inferences about food location in Tonkean macaques. *Primate Rep* 72:76
- Povinelli DJ, Eddy TJ (1996a) Factors influencing young chimpanzees' (*Pan troglodytes*) recognition of attention. *J Comp Psychol* 110:336–345
- Povinelli DJ, Eddy TJ (1996b) What young chimpanzees know about seeing. *Monographs of the Society for Research on Child Development*, Chicago
- Sabbatini G, Visalberghi E (2008) Inferences about the location of food in capuchin monkeys (*Cebus apella*) in two sensory modalities. *J Comp Psychol* 122:156–166
- Santos LR, Nissen AG, Ferrugia J (2006) Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Anim Behav* 71:1175–1181
- Schloegl C, Kotschal K, Bugnyar T (2007) Gaze following in common ravens, *Corvus corax*: ontogeny and habituation. *Anim Behav* 74:769–778
- Schmitt V, Fischer J (2009) Inferential reasoning and modality dependent discrimination learning in olive baboons (*Papio hamadryas anubis*). *J Comp Psychol* 123:316–325
- Shaw RC, Clayton NS (2013) Careful cachers and prying pilferers: Eurasian jays (*Garrulus glandarius*) limit auditory information available to competitors. *Proc R Soc B* 280:20122238
- Stulp G, Emery NJ, Verhulst S, Clayton NS (2009) Western scrub-jays conceal auditory information when competitors can hear but cannot see. *Biol Lett* 5:583–585

- [Suddendorf T, Whiten A \(2001\) Mental evolution and development: evidence for secondary representation in children, great apes, and other animals. Psychol Bull 127:629–650](#)
- [Téglás E, Gergely G, Kupán K, Miklósi A, Topál J \(2012\) Dogs' gaze following is tuned to human communicative signals. Curr Biol 22:209–212](#)
- [Tempelmann S, Kaminski J, Liebal K \(2011\) Focus on the essential: all great apes know when others are being attentive. Anim Cogn 14:433–439](#)
- [Thierry B, Anderson JR, Demaria C, Desportes C, Petit O \(1994\) Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In: Roeder JJ, Thierry B, Anderson JR, Herrenschildt N \(eds\) Current primatology. Social Development, Learning and Behaviour, vol 2. Université Louis Pasteur, Strasbourg, pp 103–117](#)
- [Tomasello M, Call J, Hare B \(1998\) Five primate species follow the visual gaze of conspecifics. Anim Behav 55:1063–1069](#)
- [Vick SJ, Anderson JR \(2000\) Learning and limits of use of eye gaze by capuchin monkeys \(*Cebus apella*\) in an object-choice task. J Comp Psychol 114:200–207](#)